HABITAT DISTRIBUTION OF SYMPATRIC POPULATIONS OF SELECTED LAMPSILINE SPECIES (BIVALVIA:UNIONOIDA) IN THE WACCAMAW DRAINAGE OF EASTERN NORTH AND SOUTH CAROLINA

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ABSTRACT

Lampsilis sp., *Lampsilis crocata* (Lea), and *Leptodea ochracea* (Say) occupied the same general habitat in Lake Waccamaw, Columbus County, North Carolina during 1979–1982. Average densities of living specimens per m^2 in Lake Waccamaw were: *Lampsilis* sp. = 1.6; *L. crocata* = 0.4; and *Leptodea ochracea* = 2.9. A slight gregariousness between Lampsilinae species was noted. Cause of minor density distribution pattern differences existing between species was not explained by data from correlation analyses of species density on basis of environmental habitat or sediment characteristics. Density related to dominant habitat vegetation was examined. *Lampsilis* sp. and *L. crocata* had highest densities in the deep sand lake regions and lowest densities in shallow sand and peat regions, but *Leptodea ochracea* differed by having a homogenous density throughout the lake; a homogeneity validated by Kruskal-Wallis (nonparametric) analysis. All three species were bradytictic. *Lampsilis* sp. and *Leptodea ochracea* became gravid September-December; the former possibly becoming gravid before the latter. Gravid condition ended after June of the following year in all three species.

The term sympatric defines two or more populations, the individuals of which are physically capable of encountering one another with moderately high frequency. Sympatric populations may have different breeding seasons and be ecologically segregated as long as a high potential exists for encounter between individuals of each population (Futuyma and Mayer, 1980). Purchon (1968) suggests that sympatric species are not closely related to each other having developed adequate barriers to interbreeding before coexisting with each other.

Sympatric naiad species of the same genus or closely-related genera are not uncommon (Ahlstedt, 1980; Emberton, 1980; Havlik and Marking, 1980; Sickel, 1980; Keferl, 1981). Discussion of naiad sympatric species and their ecological interrelationships is less common.

The sympatric *Elliptio* populations in Lake Waccamaw, Columbus County, North Carolina are perhaps best documented (Morrison, 1972; Davis et al., 1981). Recent unpublished survey data of Porter demonstrates that of the four species discussed by Davis et al. (1981) [*Elliptio waccamawensis* (Lea, 1863), *Elliptio cistelliformis* (Lea, 1863)[1], *Elliptio lanceolata* (Lea, 1828) ss.[2], *Elliptio folliculata* (Lea, 1838)] only *E. waccamawensis* is common in the lake and the other three species are relatively uncommon (Table 1). Because of these low densities, frequency of encounter between these species in the lake should be low.

A Lake Waccamaw sympatric relationship, probably having a greater frequency of encounter than that occurring within the *Elliptio* populations, includes the second, third, and fourth commonest naiads in the lake, all Lampsilinae. In decreasing order of density they are: *Leptodea ochracea* (Say, 1816), *Lampsilis* sp., and *Lampsilis crocata* (Lea, 1841)

[1] Name believed to be a synonym of *Elliptio raveneli* (Conrad, 1834).
[2] Name of Lake Waccamaw form is now *Elliptio producta* (Conrad, 1836) according to Davis or *Elliptio fisheriana* (Lea, 1838) as determined by Stansbery (personal communication).

Table 1. Lake Waccamaw naiads, their density, order of density in the lake and normality of density data.

Naiads*	Descending naiad density order #'s	Density: $\bar{X}/m^2$	Normality of density data** Skewness (*t*-value)	Kurtosis (*t*-value)
Elliptio waccamawensis	1	22.79	1.59 (12.5)	2.43 (9.6)
Elliptio fisheriana	5	0.17	9.11 (71.7)	98.75 (388.8)
Elliptio raveneli	7	0.10	9.96 (78.4)	104.65 (412.0)
Elliptio folliculata	8	0.09	5.83 (45.9)	32.04 (126.1)
Leptodea ochracea	2	2.92	1.98 (15.6)	5.78 (22.8)
Lampsilis sp.	3	1.55	3.61 (28.5)	16.87 (66.4)
Lampsilis crocata	4	0.38	5.05 (39.7)	30.63 (120.6)

*Not included are *Anodonta teres* Conrad (order #6, density = $0.14/m^2$), *Toxolasma pullus* (Conrad) (order #9, density = $0.02/m^2$), and *Villosa ogeecheensis* (Conrad) (order #10, density = $0.01/m^2$).
**t-values > t 0.01, α = 2.81 indicating non-normality.

(Table 1)[3]. This paper explores the available Lake Waccamaw data on the sympatric interrelationships between *Leptodea ochracea*, *Lampsilis* sp., and *Lampsilis crocata*.

MATERIALS AND METHODS

Description of Lake Waccamaw, its geographical location (Fig. 1), and methods used are discussed by Porter and Horn (1980) and Horn and Porter (1981). The lake bottom was divided into four sampling regions: "shallow sand" (< 1 m depth), "intermediate sand" (1–3 m depth), "deep sand" (> 3 m depth), and "peat." Each region was divided into subregions based on directional location from the center of the lake (regions and subregions are illustrated in Fig. 1, Horn and Porter, 1981). Attempts were made to sample regions equally and randomly. Three hundred and seventy-seven quantitative benthic samples were taken from Lake Waccamaw during 1979–1981. Figures 2–4 illustrate randomness of sampling. Additional non-quantitative samples were taken from Big Creek and Waccamaw River (Fig. 1). Physical data collected at sample sites included: depth, surface and bottom water temperatures, dissolved oxygen, light penetration, chlorophyll *a*, pH, dominant plant community, and sediment. Sediment samples were analyzed for percent organic matter and percent carbonate fraction. Graphic mean sediment size, sediment graphic standard deviation, sediment graphic skewness, and sediment graphic kurtosis were determined from each sediment sample (see Folk, 1974). Identifications of naiads follow suggestions by Stansbery (personal communication)[4] [see also Horn and Porter (1981) and Porter and Horn (1980)]. Representative specimens of each species have been accessioned into the mollusk collections of the Museum of Zoology, Ohio State University and the University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, North Carolina. Data analysis used SAS-BMDP interactive statistical programs in the University of North Carolina Computation Center. A Kruskal-Wallis (non-parametric) one way analysis of variance test was used after it was noted that much of the data was not distributed normally [see Dixon and Brown (1979) and Sokal and Rohlf (1969)].

[3]Other Lampsilinae existing in Lake Waccamaw [*Toxolasma pullus* (Conrad, 1838) and *Villosa ogeecheensis* (Conrad, 1834)], part of this Lampsilinae sympatric group, are not included in this discussion because of the lack of data collected about them ($\bar{X}$ densities of each = < $0.02/m^2$).

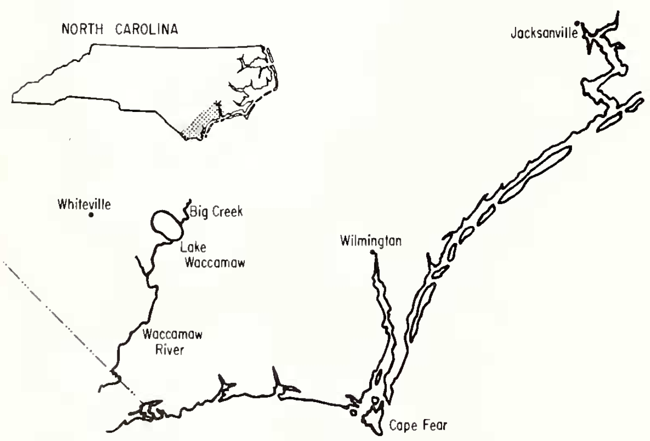

Fig. 1. Relative location of Lake Waccamaw, Big Creek and Waccamaw River in southeastern North Carolina.

[4]A paper describing *Lampsilis* sp. is in preparation by Stansbery.

RESULTS AND DISCUSSION

Density data and percent interrelationships between Lake Waccamaw Lampsilinae species are presented in Tables 1 and 2. Sixty percent of samples contain one or more lampsilines and 2.4% of the total samples had all three lampsilines.

The percent of samples having a lampsiline is increased if other lampsiline species are present. *Leptodea ochracea* was found in 48.7% of the total samples, yet 63.4% of the samples having *Lampsilis* sp. and 58.6% of samples having *L. crocata* contained *Leptodea ochracea* (Table 2). These percent increases are significant at the 5% level:(X^2 = 6.45; $X^2_{0.05,\ 1}$ = 3.84). Twenty-five percent of the total samples contained *Lampsilis* sp. but 34.5% of the samples with *Leptodea ochracea* and 44.8% of the samples with *L. crocata* had *Lampsilis* sp. (Table 2); percent increases are highly significant at the 1% level (X^2 = 25.74; $X^2_{0.01,\ 1}$ = 6.63). To a slight degree a similar pattern also occurs with *L. crocata*; 8.1% of total samples had the species, but 9.4% of *Leptodea ochracea* and 14% of *Lampsilis* sp. samples had *L. crocata* (significant at 5% level: X^2 = 4.51; $X^2_{0.05,\ 1}$ = 3.84). This increase in percent of samples containing a lampsiline suggests a gregariousness among Lake Waccamaw Lampsilinae.

Table 2. Percent frequencies of occurrence relationships between species of Lampsilinae in Lake Waccamaw*.

Species	*n* samples with species	% of total samples (372) with species	% of *n* without other Lampsilines	% of *n* with an additional Lampsiline	% of *n* with both other Lampsilines	% of *n* with *Leptodea ochracea*	% of *n* with *Lampsilis* sp.	% of *n* with *Lampsilis crocata*
Leptodea ochracea	181	48.7	63.0	32.0	5.0	XX	34.5	9.4
Lampsilis sp.	93	25.0	32.6	58.1	9.7	63.4	XX	14.0
Lampsilis crocata	29	8.1	27.6	41.4	31.0	58.6	44.8	XX

*60% of total samples contained one or more lampsiline species.
2.47% of total samples contained all three lampsiline species.

Partial correlation analyses found no significant correlation between the lampsilines treated (Table 3). Sample density data that these analyses used was not normally distributed (Table 1, note the large numbers of samples without Lampsilinae and the high *t*-values for sample skewness and kurtosis values). Scatter diagrams comparing densities of lampsiline species against each other (not included here) provided no indication of any pattern between species.

Correlations of species density with physical habitat data and other Lake Waccamaw mollusk species densities gave results of unknown implication (Table 3). *Lampsilis* sp. and *Leptodea ochracea* populations are highly correlated with the *Elliptio waccamawensis* population (1% level). These correlations may be related to the similarity of the regional density pattern of *E. waccamawensis* which resembles the pattern of *Lampsilis* sp. (Fig. 2). Both *Lampsilis* sp. and *E. waccamawensis* are similar in that both are endemic to Lake Waccamaw; these two species and *Leptodea ochracea* are comparable as Lake Waccamaw is the only known North Carolina body of water containing major populations of all three [note Fuller (1977) comments on *Leptodea ochracea*].

Table 3. Significant correlation summary (5 & 1% levels) for 1979–1981 Lake Waccamaw physical and molluscan density by Lampsilinae species data. Data developed from partial correlation matrix. N (=294) samples used in analyses. For physical data, only significant correlation included; 1% level indicated by "*"; $r_{0.01,\ 300}$ = 0.148, $r_{0.05,\ 300}$ = 0.113 *(Snedecor, 1956); high level of significance by partial correlation coefficients indicated when data is 1.5 times r* level of significance, thus significant correlation is indicated when $r_{0.01} > 0.222$ or $r_{0.05} > 0.170$ (Reish, personal communication).

Lampsilinae sp.	vs. Species densities and physical data correlations	Partial correlation coefficients
Lampsilis sp.	*Lampsilis crocata*	0.116
	Leptodea ochracea	−0.023
	Elliptio waccamawensis	0.316*
	No physical data correlations	
Lampsilis crocata	*Lampsilis* sp.	0.116
	Leptodea ochracea	−0.008
	No physical data correlations	
Leptodea ochracea	*Lampsilis* sp.	−0.023
	Lampsilis crocata	−0.008
	Elliptio waccamawensis	0.304*
	pH	−0.194

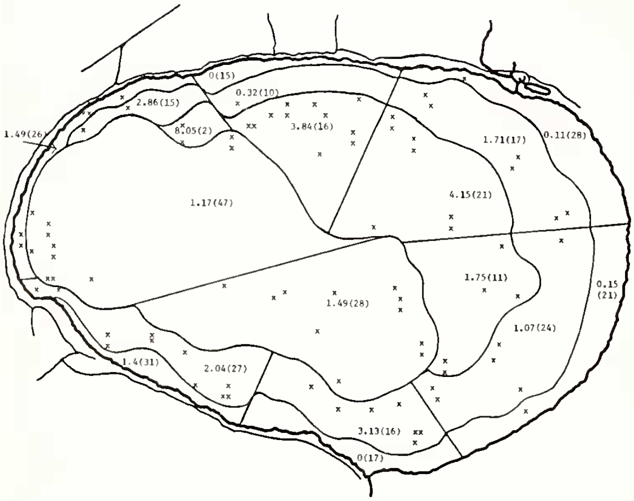

Fig. 2. Mean density, by subregion, of *Lampsilis* sp. in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *Lampsilis sp.*

Significant, but negatively correlated with *Leptodea ochracea* was pH (5% level); pH was the only measured chemical or physical parameter significantly correlated with any of the three Lake Waccamaw species of Lampsilinae. The relationship suggests that Lake Waccamaw *Leptodea ochracea* increase in density as acidity increases. Johnson (1970) recorded specimens of this species in the lower Waccamaw River, an area of probable higher acidity than Lake Waccamaw. Collections made by the senior investigator in the lower to mid Waccamaw River areas and in the lower Big Creek (Fig. 1) during 1979–1982 did not contain this species. Both of these Waccamaw drainage habitats contain mollusks but at times have pH values lower than those measured for Lake Waccamaw. Additional evidence of a tolerance by this species for pH values lower than that present in Lake Waccamaw was not found.

Mean densities of Lampsilinae species to dominant plant association are shown on Table 4. Density of *Lampsilis* sp. and *Leptodea ochracea* seem unaffected by Spatterdock [*Nuphar luteum sagittifolium* (Walt) E. O. Beal], which lines the shallow northern shores of the Lake, and Najas [*Najas quadalupensis* (Spring.) Magnus], a plant found principally in the peat substratum of the lake. Their density does seem reduced by: Maidencane (*Panicum hemitoman* Schul.), which lines the shallow southern lake shores; *Plectonema* sp., a blue-green algae; and an unidentified grass-like plant found along the lake shores. *Leptodea ochracea* density also appears adversely affected by the Maidencane and *Plectonema* beds. Density of this species increased where Spatterdock and the unknown grass-like plants occurred. No

Table 4. Mean 1978–1981 Lampsilinae density data by dominant plant associations*, Lake Waccamaw, North Carolina. General statistics included: "N" = number of samples; "% = 0" indicates percent of samples having a zero density value. All data had high skewness and kurtosis values indicating data of a non-normal condition. Comparisons in text contrast average (mean) lampsiline "No plant" condition density vs. mean density of lampsiline species where a plant association is noted.

Lampsilinae Dominant Plant	Mean Density	Standard Deviation	Standard Error	N	% = 0	Range
Lampsilis sp.						
Unknown	2.10	3.627	0.324	125	62.4	0.0–22.6
No plants	1.70	3.949	0.346	130	76.9	0.0–22.6
Maidencane	0.17	0.734	0.121	37	94.6	0.0– 3.2
Spatterdock	1.76	3.111	0.663	22	68.2	0.0– 9.7
Najas	1.46	5.099	0.888	33	78.8	0.0–29.0
Plectonema	0.00	—	—	12	100.0	—
?Grass-like	0.00	—	—	13	100.0	—
Lampsilis crocata						
Unknown	0.59	1.980	0.177	125	88.0	0.0–12.9
No plants	0.35	1.324	0.116	130	92.3	0.0– 8.3
Maidencane	0.00	—	—	37	100.0	—
Spatterdock	0.29	1.386	0.295	22	95.5	0.0– 6.5
Najas	0.39	1.343	0.234	33	90.9	0.0– 6.5
Plectonema	0.00	—	—	12	100.0	—
?Grass-like	0.25	0.888	0.246	13	92.3	0.0– 3.2
Leptodea ochracea						
Unknown	2.78	3.448	0.308	125	48.8	0.0–16.1
No plants	3.48	4.679	0.410	130	48.5	0.0–25.8
Maidencane	1.72	2.722	0.447	37	67.6	0.0– 8.3
Spatterdock	4.58	5.854	1.248	22	40.9	0.0–19.4
Najas	2.63	3.372	0.587	33	45.5	0.0–12.9
Plectonema	0.00	—	—	12	100.0	—
? Grass-like	7.73	3.196	0.887	13	46.2	0.0– 3.7

*Plant associations:
- Unknown = Dominant plant at collection site not determined.
- Maidencane = *Panicum hemitomon* Schul.
- Spatterdock = *Nuphar luteum sagittifolium* (Walt.) E. O. Beal.
- *Najas* = "Water Nymph", *Najas quadalupensis* (Spreng.) Mangus.
- *Plectonema* = Unidentified species of blue green algae.
- ? Grass-like = Mixture of unknown grass-like plants.

Lampsilinae or any naiads lived where a mat of *Plectonema* was present.

Both *Lampsilis* sp. and *Lampsilis crocata* have their greatest densities in the deep sand regions and lowest densities in shallow sand and peat regions of the lake (Figs. 2–3). This distribution is similar to that of *Elliptio waccamawensis* which has already been shown to have densities correlated with that of *Lampsilis* sp. In addition the high density area of *L. crocata* includes intermediate sand subregions.

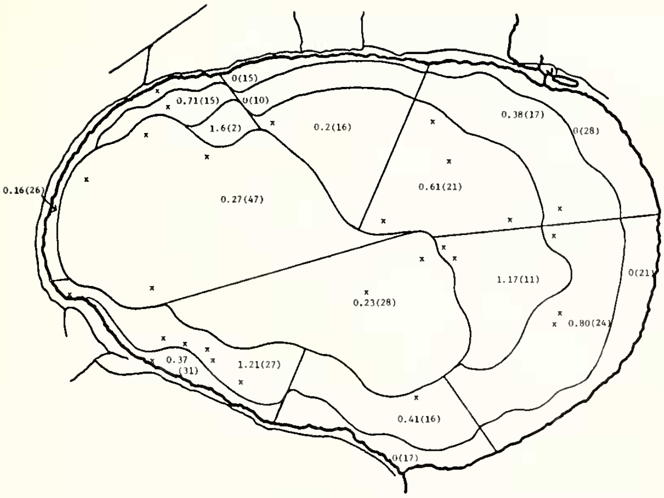

Fig. 3. Mean density, by subregion, of *Lampsilis crocata* in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *L. crocata*.

Distribution of *Leptodea ochracea* (Fig. 4) differed from that of the other two *Lampsilis* species by not having a regional or subregional pattern. This regional density homogeneity was validated by Kruskal-Wallis (nonparametric analysis of the data (Table 5). The same analysis indicated heterogeneity for the regional density data of both *Lampsilis* sp. and *L. crocata*. Physical factors affecting the species

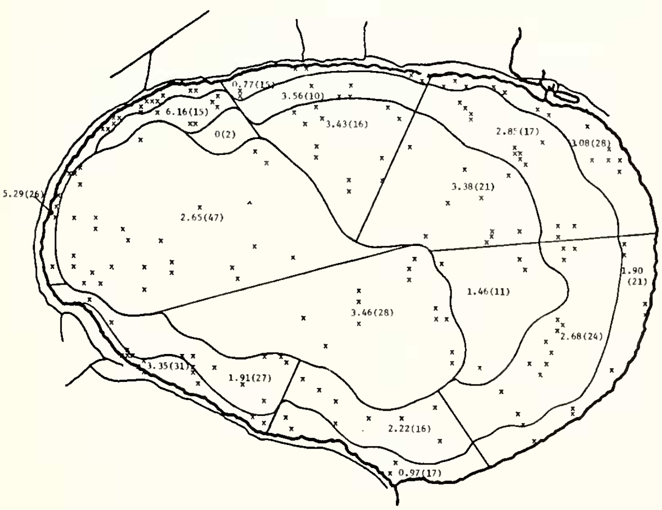

Fig. 4. Mean density, by subregion, of *Leptodea ochracea* (Say) in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *Leptodea ochracea*.

Table 5. Kruskal-Wallis (non-parametric) one way analysis of variance test results of 1978–1981 Lake Waccamaw ranked regional data by species of Lampsilinae. Test description in Dixon and Brown (1979) and Sokal and Rohlf (1969). Number of samples = 338. Levels of significance less than 0.01 suggest that the data is not homogenous (heterogenetic) throughout the four Lake Waccamaw regions, such values are indicated by an "*".

Variable	Kruska-Wallis Test Statistic	Level of Significance (chi-square distribution, 3 degrees freedom)
Lampsilis sp.	38.05989	0.0000*
Lampsilis crocata	15.90010	0.0012*
Leptodea ochracea	0.46155	0.9273

density homogeneity of Lampsilinae within the Lake Waccamaw regions or subregions have not been identified by this study.

Species of the three Lampsilinae are known to be bradytictic. This breeding pattern was verified by the collection of gravid females of each species during winter months. Gravid *Lampsilis* sp. were collected during: September, December, March, April, and June. Gravid *Leptodea ochracea* were seen in Lake Waccamaw only in March and June. Gravid *Leptodea ochracea* were collected in Lake Waccamaw during December, February, March, April, May, and June. Ortmann (1919) listed October, November and June as months when *Leptodea ochracea* were gravid; Johnson (1970) also lists May. The period of gravid condition for *Lampsilis* sp. in Lake Waccamaw is indicated as beginning around September and ending after June of the following year. Gravid period of *L. crocata* could not be determined because not enough data was present, however the period possibly ends after June. The period of gravid condition for *Leptodea ochracea* in Lake Waccamaw may begin later than that of Lake Waccamaw *Lampsilis* sp.; first gravid *Leptodea* were not seen in September but were seen later in December. The gravid period for the species is believed to end after June of the following year. Samples of species of Lampsilinae were not large enough in any given lake area or time period to allow differences between periods of gravid condition to be judged as real or as a manifestation of interspecies variation.

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